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FLORAL SUCCESSION IN THE PRAIRIE-GRASS FORMATION OF SOUTHEASTERN SOUTH DAKOTA

SEROTINAL AND AUTUMNAL FLORAL ASPECTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 117

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(WITH FOUR FIGURES)

Serotinal floral aspect

Climatologically and florally the serotinal is perhaps the most distinctly demarked of the aspects. The climatological changes which set it off from the estival are quite generally appreciated, while the general blooming of the pioneer sod-formers during the early part of July with the accompanying serotinal bloomers no less distinctly marks it in a floral way.

One records now less dissimilarity in aspect and tone on crest, slope, and base; the more open association, however, still marks the crest. The tone is determined by the dull-greenish vegetative stalks of *Solidago rigida* and *Helianthus Scaberrimus*, which occur copiously throughout the formation. It is relieved locally on lower slopes by the yellow of *Ratibida columnaris* and on upper slopes by the blue of *Verbena stricta* and the canescence of *Amorpha*; while *Meriolix serrulata*, *Brauneria pallida*, *Potentilla Hippiana*, *Erigeron ramosus*, *Polygala alba*, and *Euphorbia marginata*, all of which extend over from the estival, are less influential. A few conspicuous forms are added in this aspect, but never of sufficient abundance to strongly variegate the dull green of the tone given by the leafy stems of *Solidago* and *Helianthus*.

The general flowering of *Agropyron occidentale*, *Bulbils dactyloides*, and the *Boutelouas*, together with *Kuhnistera purpurea* and *K. candida*, distinctly marks the inception of the serotinal aspect, which is characterized by the gradual appearance of few but conspicuous bloomers and the attainment of maximum flowering of late estival forms, rather than by the addition of numerous forms as in the

the chresard at a minimum are thus the ecological conditions which strongly mark the serotinal floral aspect.

SPECIES OF THE SEROTINAL FLORAL ASPECT

FACIES.—*Bouteloua oligostachya*,† *B. hirsuta*,† *B. curtipendula*,† *Bulbilis dactyloides*.*†

PRIMARY SPECIES.—*Kuhnistera purpurea*,† *Verbena stricta*,*† *Ratibida columnaris*,*† *Kuhnistera candida*,† *Symphoricarpos occidentalis*,*† *Amorpha canescens*.*†

SECONDARY SPECIES.—*Agropyron occidentale*, *Carduus undulatus*,* *Euphorbia marginata*,* *Hymenopappus filifolius*, *Calamovilfa longifolia*, *Polygala alba*.*

TERTIARY SPECIES.—*Lygodesmia juncea*, *Lacinaria squarrosa*, *Brauneria pallida*,* *Meriolix serrulata*,* *Eriocarpum spinulosum*, *Erigeron ramosus*,* *Potentilla Hippiana*.*

RUDERAL SPECIES.—*Cassia chamaecrista*, *Onagra biennis*, *Amaranthus graecizans*, *Melilotus alba*,* *Chenopodium album*, *Lactuca canadensis*, *Apocynum cannabinum*.

*From previous aspect. †Forming associations.

Agropyron occidentale is the first of the serotinal grasses to bloom. It is a xerophytic bunch-grass and occupies prairie crests, where it occurs copiously, rarely even of facial rank. It is one of the pioneers of the bunch-grass stage and is associated with the *Andropogons*, passing with these forms as they give place to the *Boutelouas* and being entirely absent in the older and more mesophytic prairie. In transitional stages from the bunch-grass open association to the less xerophytic closed sod association, *Agropyron* remains not infrequently in subcopious abundance as a relict of the earlier condition. The rootstock is here an efficient mode of propagation.

The three grama grasses, *Bouteloua hirsuta*, *B. oligostachya*, and *B. curtipendula*, which head out during the early days of July, enter upon anthesis almost simultaneously with the beginning of the second week of July, as does also the buffalo grass, *Bulbilis dactyloides*. The *Boutelouas* are pioneer sod-formers, following only the buffalo grass, which as the pioneer sod-former encroaches upon the bunch-grasses, replacing them and preparing the way for the *Boutelouas* which invariably follow closely. To the west, where the rainfall is much less, *Bulbilis* is the prominent sod-former and is the fodder grass of the great cattle ranges west of the Missouri. In our region it occurs along the xerophytic exposures of the bluff line, and as a

xerophytic relict along the crest of prairie knolls, where it mingles with the gramas as they advance upon the bunch-grass stage, yet usually as a secondary element among these sod-formers. In our area, however, it is lacking.

Bouteloua hirsuta seems to be the pioneer of the gramas as they encroach upon *Bulbilis*, or upon the bunch-grasses where *Bulbilis* is absent, as is the case in our formation. It is in turn apparently



FIG. 1.—Serotinal aspect: *Bouteloua curtipendula* sod on upper slope; *Solidago rigida* to the left; *Helianthus scaberrimus* to the right; admixture in the background.

followed by *B. oligostachya*, which seems to occur more abundantly and to occupy the most prominent place of the sod-formers. Frequently it alone encroaches upon the bunch-grasses, *B. hirsuta* being absent. Next comes *B. curtipendula* (fig. 1), which also contributes largely to the early prairie sod. In many places the *Poa* sod is the next to follow. The gramas are thus largely confined to the crests, decreasing in abundance downward, where they not infrequently rise to facial prominence. Contrary to the serotinal floral forms, the *Boutelouas* are of low stature, *B. curtipendula* alone rising above

45^{cm}, which however may frequently reach 60 to 80^{cm}, and is the only species which becomes at all conspicuous. These species as they enter the open bunch-grass association form mats, which fusing form sod, finally resulting in the replacement of the bunch-grasses. The gramas are all perennial by means of the enlarged rootstocks.

Coincident with the flowering of the grasses is that of *Kuhnistera purpurea*, which seems to precede that of its related species *K. candida* by only a few days. The purple *Kuhnistera* is from its distribution and structure more xerophytic than the white-flowered species. The former occurs most abundantly on the higher slopes, decreasing in abundance downward; while the latter reaches its maximum abundance on the lower slopes, decreasing in the number of individuals per unit area upward. Along middle slopes the abundance of the two species approaches equality. Its distribution seems clearly related to the chresard of these various habitats. CLEMENTS ('05, pp. 233) in light of these facts has suggested the monophyletic origin of these two species from an ancestral form which became split up into *purpurea* and *candida* under the influence of and adaptation to a low and high chresard, a xerophytic and mesophytic habitat respectively, and has instituted experiments to test this theory. In their respective positions of maximum abundance each may rise to dominance, which, however, never occurs in the plot under study; the advanced condition of the prairie seemingly precludes such abundance in the closed association. However, they are the most conspicuous elements of the early part of the aspect. Their branching stalks rise 60 to 80^{cm} and are terminated by cylindrical spikes (some 8 or 9^{cm} long) of white flowers in *K. candida* and (some 5^{cm} long) of violet flowers in *K. purpurea*. They are perennials from thick and deep roots. The seeds are immobile, which with the perennial root accounts for their somewhat even distribution in the formation.

With the prairie clovers appear *Eriocarpum spinulosum* and *Lygodesmia juncea*. *Eriocarpum* is perennial from a deep woody root, whose much-branched stems rise about 30 to 40^{cm}, terminate in 1 to 25 heads fringed with yellow rays and 2.5^{cm} in diameter. In all it is very striking, but its rare occurrence along upper slopes and crests precludes more than a minor influence upon the tone. It

seems to demand only a low chresard, and upon more xerophytic crests than occur in our formation, where it holds its own, it appears copiously and not infrequently determines the tone of the open association. The wind-distribution is facilitated by a copious pappus. Perhaps no plant of our formation has the remarkable degree of adaptability possessed by *Lygodesmia juncea*. The first plant to appear upon the bare exposed soil of bluffs, it persists into a well-formed mesophytic sod with even a marked abundance. It is to be reckoned as a xerophytic relict in our plot, occurring most abundantly along the crest, but at most only sparsely. It is a perennial from a heavy woody root, which interprets its persistence in the formation, and this with its reduced scalelike leaves contributes to its fitness as a pioneer xerophyte. The much-branched stems (45^{cm} high) end in solitary pink-rayed flowers, whose small size and ephemeral duration never render them florally conspicuous. Distribution is very general and wide; the achenes are provided with a copious pappus.

During the last days of the second week and early in the third week of July the prairie thistle, *Carduus undulatus*, enters upon anthesis and florally characterizes this part of the aspect. Its densely white tomentose and much-branched stems rise some 90^{cm} and terminate in large (5^{cm} in diameter) solitary heads of numerous purplish flowers. It also assumes a gregarious habit, and patches occur here and there from base to crest of prairie slopes. Thus it is a most conspicuous form, but reaches its maximum flowering only in early August. Wherever the prairie sod has been disturbed it becomes almost exclusive in its occupancy. It is a biennial of slightly mesophytic tendencies and so appears more commonly on lower slopes. Its high fertility and copious pappus insure a wide distribution, easily explaining its very general occurrence.

The last form to be added in the aspect is *Lacinaria squarrosa*, which appears here and there upon upper slopes and crests. It is very xerophytic in nature, occupying a prominent place in the early stages of the bluff line succession, and is in our plot to be considered as a relict. It is not conspicuous and adds little to the tone, which is at this time rendered bizarre by several of the earlier forms now in their greatest floral display. *Lacinaria* is an erect (50^{cm}) perennial

herb from a tuberous structure, terminating in a spike bearing numerous heads of purplish flowers. The abundant plumose pappus assures a widespread distribution.

Autumnal floral aspect

No marked climatological change is to be noted in passing from the serotinal to the autumnal aspect, but simply one of gradually decreasing favorableness. Hence the latter has been set off partly for convenience of discussion, though it seems more or less distinctly characterized by definite floral activity; yet possibly it might be more accurately designated as late serotinal. Beginning in early August and marked by the estivation of such very conspicuous forms as *Helianthus scaberrimus*, *Solidago rigida*, and the bunch-grasses (*Andropogon furcatus* and *A. scoparius*), it extends into early October, when vegetative activity comes to an end. Its floral activity is terminated, however, in middle September by the flowering of *Gentiana puberula* and *Solidago rigidiuscula*, while florally the aspect is at its best during late August and early September, when the prairie is a sea of yellow from the Solidagos, mainly *S. rigida*, dotted here and there by the blue of Asters. Rising sentinel-like along higher slopes and crests are the rose-purple spikes of the blazing-stars, while on isolated knolls associations of *Aster sericeus* with their purplish flowers and white tomentose leaves relieve the sea of yellow. The bunch-grasses impart a very characteristic tone to the higher and more xerophytic knolls.

In earlier aspects marked restriction of forms was noted, less apparent in the serotinal it is here scarcely evident. On the other hand there is a marked identity of the controlling species on base, slope, and crest, the entire formation presenting an unbroken and identical covering, undoubtedly to be associated with the noticeable equality of the chresard throughout these various situations.

Eighteen of the twenty-two forms (82 per cent.) are composites, and all but one of these (*Kuhnistera villosa*) are wind-distributed. Like the preverinals the autumnals are pronouncedly xerophytic, fitting into uncertain, that is unfavorable, ecological conditions, the former at the initiation, the latter at the decline of floral activity. Just as preverinals have come to possess the spring period of not

so largely accomplished. However, the climatological conditions (table) of this aspect bear to its floral activity a relation analogous to that existing in the prevernal, and the forms here occurring seem in no less degree peculiarly adapted to the late seasonal conditions.

In August the wind is dominantly from the south and east, but in early September begins to swing to the northeast quadrant, where it remains until the prevernal, then swinging round again to the south-east. The average daily rainfall (0.26^{cm}) remains about the same as in the preceding aspect, though it falls on only 25 per cent. of the days, while in the serotinal it falls on 33 per cent. of the days. Relative humidity, sunshine per cent., and relative light intensity are noticeably similar in these two aspects, while relative evaporation has decreased almost a third. In the fact that the hourly wind velocity has increased only a tenth, and in the 4° C. fall in the mean temperature must be sought an explanation of this lowered evaporation.

SPECIES OF THE AUTUMNAL FLORAL ASPECT

FACIES.—*Andropogon furcatus*,† *A. scoparius*.†

PRINCIPAL SPECIES.—*Solidago rigida*,† *Aster sericeus*,† *Helianthus scaberrimus*,† *Sporobolus brevifolius*.†

SECONDARY SPECIES.—*Solidago rigidiuscula*,† *S. missouriensis*, *S. nemoralis*, *Ratibida columnaris*,*† *Aster multiflorus*, *Artemisia gnaphaloides*,* *Verbena stricta*,*† *Carduus undulatus*.*†

TERTIARY SPECIES.—*Aster oblongifolius*, *Solidago canadensis*,† *Kuhnia glutinosa*, *Lacinaria scariola*, *Nabalus asper*, *Lygodesmia juncea*,* *Polygala alba*,* *Dysodia papposa*, *Grindelia squarrosa*, *Kuhnia eupatorioides*, *Lacinaria punctata*, *Gentiana puberula*, *Kuhnistera villosa*, *Meriolix serrulata*.*

RUDERAL SPECIES.—*Salsola tragus*, *Melilotus alba*,* *Lactuca canadensis*.*

*From earlier aspect.

†Forming associations.

During the early days of August four forms, destined later to become very conspicuous, make their floral appearance in the following order: *Solidago missouriensis*, *Helianthus scaberrimus*, *Solidago nemoralis*, and *S. rigida*. *S. missouriensis*, the first of the autumnal bloomers, occurs in subcopious abundance and most abundantly in the open association of the upper slopes and crests, where it is quite noticeable, though it never becomes a prominent feature of the tone because of its low stature and small panicles. It is distinctly xerophytic, as is evident both by its structure and distribution, and, as

might be inferred, passes as the open formation gradually becomes closed, never being present in a compact sod at the base of the slope.

Appearing with *S. missouriensis* comes *H. scaberrimus*. It occurs both more frequently and abundantly than the former and is distinctly less xerophytic, reaching its greatest abundance upon middle and upper slopes. Its rigid, rough, and little-branched shoots, rising some 1.5^m and terminated by a spreading corymb bearing

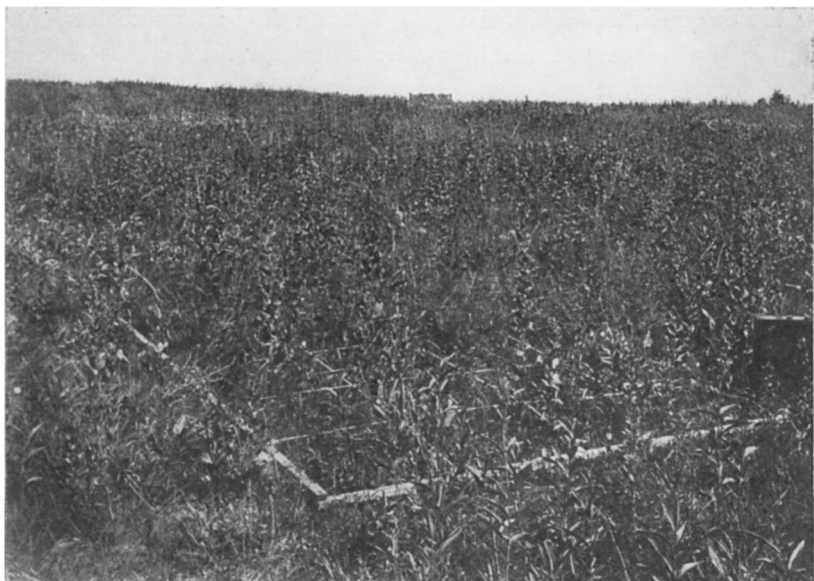


FIG. 2.—Late serotinal aspect: *Solidago rigida* and *Helianthus scaberrimus* on upper slope.

few conspicuous heads (3 to 5^{cm} wide) with numerous yellow rays, make it a conspicuous element of the early autumnal aspect, but it soon blends in the sea of yellow of *Solidago rigida*, which shortly comes on, completely dominating the floral tone. *Helianthus* (fig. 2) rarely holds its own along the tension line where the *Poa* sod is encroaching, but with other open association forms yields to its advancement, though it occurs inclusively in the less compact sods higher up the slopes, in which places it frequently assumes a copio-gregarious habit. The stiff sunflower is perennial by a thick root-

stock. A very limited pappus of two to four scalelike awns provides only a restricted distribution, easily accounting for its gregarious tendency.

About a week or ten days later *S. rigida* begins its blooming, but only reaches its maximum about the last of the month, at this time solely characterizing the floral tone and maintaining a sea of yellow for some three weeks, when the tone begins to pale as fruiting advances and completely gives way during the third week of September, the bright-yellow floral tone yielding to the dull-green foliage. The stiff goldenrod occurs ubiquitously, but reaches its greatest abundance upon middle slopes, where it is frequently copious. The single stout stem (frequently several), from the perennial rootstock, rises somewhat over a meter, terminating in a flat dense cyme bearing numerous yellow-rayed flowers, frequently 20 to 25^{cm} across, which with its abundance and frequency makes *S. rigida* the most striking and dominating in its floral tone of any single species of the formation. Following the latter species by only a few days *S. nemoralis* comes into bloom. Overtopped by and much less abundant than the former, it never is conspicuous, though frequently it adds to the dominant yellow tone of the aspect. It reaches its greatest abundance on slopes, occasionally entering the open association of the crests, but is rarely included in the compact sod of lower slopes.

The three goldenrods just noted are alike perennial from a thickened rootstock, with a tendency toward the formation of perennial basal rosettes, and are widely wind-disseminated through the efficiency of the well-developed parachute.

Almost coincident with the blooming of these four forms is that of the bunch-grasses, *Andropogon furcatus* and *A. scoparius*. Though these two grasses during the last two aspects have been vegetatively conspicuous upon the higher crests and most xerophytic slopes, where they contribute the characteristic dull tone to the bunch-grass association, they flower only during the early part of August, thereby adding but little to their already established prominence. They are accompanied by *Sporobolus brevifolius*, which occurs less abundantly, but like the beard-grasses assumes the bunch habit upon higher crests and ridges. In these situations the Andropogons assume facial rank, *A. furcatus* (fig. 3) being the taller and on account of its

invariable bunch habit far the more conspicuous. *A. scoparius* (fig. 4) seems to form a very loose sod between the bunches of the former and extends lower down upon the slope, where in places it yields to the Boutelouas or rarely to *Poa*. In succession these forms seem to precede the Boutelouas. With a reduction of drainage and introduction of these sod-formers, the bunch-grasses yield, and in those portions of the prairie where succession has progressed most



FIG. 3.—Autumnal aspect: the bunch-grass, *Andropogon furcatus*, with intervening spaces occupied by Bouteloua sod near crest of prairie knoll.

rapidly, for example the northwestern exposure, the Andropogons and the "bunch-habit" are conditions of the past. With *Agropyron occidentale*, the Andropogons and *Sporobolus* must be ranked as the pioneer grasses of the prairie, and as such hold a most important ecological relation in the structure and development of the formation. *A. furcatus* yields first, giving way to *A. scoparius*, which in places assumes facial abundance and frequently persists in a somewhat anomalous way in the more mesophytic associations. These grasses

are wind-distributed, to which end the hairy awned spikelets contribute. Being perennials from heavy resistant rootstocks, they are well adapted to the precarious pioneer position they occupy in the formation.

Two composites, taking a minor place in the formation, must be mentioned. While belonging to the formation proper, they function mainly as ruderals. *Dysodia papposa*, which blooms at the beginning of the autumnal aspect and often earlier, occurs everywhere along



FIG. 4.—Autumnal aspect: an *Andropogon* sod, mainly *A. scoparius*, upon crest of knoll; scattered individuals of *Solidago*, *Helianthus*, and *Aster* are present.

roadsides and on wastes, where it attains its greatest size and abundance. Frequently on the most xerophytic of prairie hills and bluffs it assumes a very marked prominence. In our area it occurs subcopiously along crests and ridges, in fact anywhere that the association may be open, though it is usually depauperate in such cases. The fetid marigold is an annual, and its ubiquity finds cause in the ease and abundance of its dispersal through an efficient pappus, and in the period of its germination falling at the time when the majority of forms have long since germinated and the formation is thinning off its early annuals and prevernal and vernal perennials. To these

reasons must further be added its high degree of adaptability for germinating under these less favorable serotinal conditions.

The other form here included is *Grindelia squarrosa*, which occurs only sparsely and then almost entirely along lower slopes and frequently included in the Poa sods. On account of its scattered distribution, the gum plant usually grows about 50^{cm} high and branches much and more or less symmetrically, so that with its many heads of yellow ray-flowers it becomes quite noticeable in early September. *Grindelia* is a perennial from a heavy rootstock. The few awned achenes are inclosed in a glutinous head, consequently distribution is restricted, and correspondingly a gregarious tendency is to be noted.

During the last two weeks of August several forms of secondary prominence in the floral tone progressively bloom. They are *Solidago canadensis*, *Lacinaria scariosa*, *L. punctata*, *Artemisia gnaphaloides*, *Kuhnia glutinosa*, and *K. eupatorioides*. *Solidago canadensis*, the most mesophytic of our goldenrods, seems to be confined exclusively to Poa sods in valleys and at the base of slopes. It is here gregarious in tendency, occurring in isolated patches or clumps. Also upon disturbed soil around coyote burrows it usually establishes itself in dense patches. It rises about a meter, with several shoots from the same large perennial rootstock, branches profusely, bearing numerous heads in dense panicles, and in all is most conspicuous along with *Grindelia* at the base of slopes and in valleys. Its distribution by well-developed pappus is extensive, though its demands for the highest ecological conditions greatly restrict its establishment.

The two button-snakeroots, *Lacinaria scariosa* and *L. punctata*, bloom about the beginning of the last week of August, and though sparse in their distribution, being confined to crests, ridges, and the open association of upper slopes, they rise like sentinels of the prairie, relieving the blaze of yellow by touches of purple. *L. scariosa* seems more mesophytic than *L. punctata*, blooming usually a few days later and upon upper slopes mainly. It is also much taller and the heads are larger than in the latter and so more prominent. The numerous short-peduncled heads of purplish flowers, borne upon the erect unbranched and usually solitary stem from a prominent tuber, give these forms a most striking appearance. Copious pappus assures a wide wind-distribution.

The prairie mugwort, *Artemisia gnaphaloides*, is gregarious upon upper slopes. Here it forms dense patches, and these, on account of the white tomentosity of its stems and leaves, which are frequently 50^{cm} high, are conspicuous in the dominant tone of yellow. It bears to the autumnal quite the relation that the *Antennarias* hold to the prevernal and vernal tone. Perennial from a tuber-like root, it is also xerophytic in tendency. In its pappate achenes and root-propagation are found the causes of its gregarious habit.

The closing days of August are marked by the estivation of the two false bonesets, *Kuhnia eupatorioides* and *K. glutinosa*. They both occur but rarely and then mainly upon upper slopes and crests. They form little clumps (several shoots from the same perennial root) and are tall (50 to 75^{cm}) and much branched, but on account of their small few-flowered heads of creamy-white color and their only occasional frequency, they never attain any prominence. However, they become much more noticeable when the rich white pappus spreads in maturation, during the second week of September. *K. eupatorioides* is more mesophytic and so occurs more frequently over the formation. *K. glutinosa*, however, is pronouncedly xerophytic, and is restricted in its distribution to the open association along crests and higher slopes. The abundant barbate pappus assures prolific invasion, though establishment seems to be very limited, doubtless due to the apparently low degree of adaptability possessed by these forms.

The *Kuhnias* are accompanied by *Nabalus asper*, which is restricted to lower slopes, is of rare occurrence and thus always a minor element. Though it is of the upper layer and bears numerous heads of pale-yellow flowers, it blends into inconspicuousness in the general tone. It is a perennial from a tuberous root. A well-developed parachute insures wide dissemination, but high ecological demands preclude more than a rare establishment upon the prairie.

The early days of September are well marked by the blooming of four forms which occasionally attain more or less restricted prominence: *Aster sericeus*, *A. multiflorus*, *A. oblongifolius*, and *Kuhnistera villosa*. They are all of evident xerophytic tendencies and occur mainly upon the upper slopes and crests. Appearing at a time when there is an apparent decline in the dominance of the earlier tone, and

occurring in the open association, the Asters become quite noticeable though they are all of a lower layer than *S. rigida*. The silky Aster, *A. sericeus*, usually of low abundance and general occurrence, frequently becomes copious on bunch-grass knolls, there forming very distinct associations. Rising some 50^{cm}, with numerous spreading branches terminating in prominent heads (2 to 3^{cm} in diameter) with numerous violet rays, and bearing abundant leaves which are densely covered above and below with a silvery-white silky pubescence, this Aster is always a conspicuous element of the middle and late autumnal aspect. Its achenes are equipped with a medium pappus. It is a perennial from a thickened rootstock.

The two other Asters are similar in frequency and abundance to *A. sericeus*, but never attain its prominence. Of these *A. oblongifolius* always occurs with *A. sericeus* in the open association. With us it always remains depauperate. Seldom more than 30^{cm} high, it is ever inconspicuous, though its bluish rays make it noticeable at short range, since it is usually overshadowed by *A. sericeus*. It is a perennial and is wind-distributed; a copious pappus serves to bring about a general invasion, which, as in the other Asters, seems to be coupled with a high percentage of establishment, especially in the open xerophytic associations of the formation. The dense-flowered aster, *A. multiflorus*, occurs perhaps more frequently but less abundantly than the former, and is similarly a xerophyte of the open association, in which situations it never reaches other than a reduced stature. However, its bushy spreading branches, thickly beset with numerous small white heads, invariably make it more prominent than *A. oblongifolius*, particularly when it occurs in patches. It seems to work down upon the lower slopes, here attaining a greater stature and abundance as well as a greater prominence in anthesis.

All the Asters are perennial from rootstocks and form small basal rosettes, and are wind-disseminated.

The hairy prairie clover, *Kuhnistera villosa*, is a perennial from a deep tuberous root. Densely silky pubescent, abundantly branched, and terminating in cylindrical clustered spikes (3 to 6^{cm} long) of rose-purplish flowers, it is in itself quite conspicuous, but its restricted frequency and rare abundance make it rarely a tonal component in the formation. In the bunch-grass formation it becomes, with *Amorpha*

canescens, more abundant but never controlling. It is distinctly xerophytic, and while largely of the open association, it may work down slopes into more favorable habitats.

During the middle days of September the last two forms of the prairie-grass association present their flowers, *Gentiana puberula* blooming a few days before *Solidago rigidiuscula*, the last form to bloom. The downy gentian occurs rarely and is largely restricted to middle and lower slopes, rarely if ever occurring along the xerophytic crests and ridges. Its terminal group of few large light-blue flowers are rendered unimportant as the plant is of short stature (30 to 40^{cm}) and so hidden. It is perennial from thickened roots, and wind-distributed, the seeds being widely winged. Its rarity therefore lies no doubt in its high ecological requirements, being somewhat mesophytic in its nature.

The last form of the prairie to bloom is *Solidago rigidiuscula*. Flowering as it does when *S. rigida* is passing into fruit, of copious abundance and high frequency upon upper slopes, occurring gregariously at times with several stalks (5 to 15) arising from the same perennial root, it is rightly named the "showy" goldenrod. It persists nearly to the middle of October, and is one of the last forms to pass into fruit, though accompanying it are the later flowers of *Meriolix*, *Ratibida*, *Carduus*, *Polygala*, and *Lacinaria*. It is widely wind-dispersed and establishment is quite general.

Post-floral aspect

By the second or third week in October the prairie forms of the autumnal floral aspect have all passed into seed, and the gorgeous yellow of *Solidago rigida* has given way to the somber brown of frosted leaves and stalks. While seed maturation and distribution in species of earlier aspects have been in progress during the subsequent aspects, the post-floral aspect, extending up into late November, is particularly characterized by this phase of plant life, yet dispersal may and does continue, but in a much more limited degree even during the winter season. The little fall of snow leaves the prairie bare the greater part of the winter, its tone being in no way modified; the post-autumnal appearance remains to characterize the prairie throughout the non-flowering period, and, as has already been pointed out,

extends up to and even dominates the prevernal and vernal floral aspects.

Summary of the structure of the formation

The formation is strictly of the prairie-grass type, its facies being determined mainly by six species: *Bouteloua oligostachya*, *B. curtipendula*, *B. hirsuta*, *Koeleria cristata*, *Andropogon furcatus*, and *A. scoparius*, to which must be added *Poa pratensis* in valleys and on lower slopes. The Andropogons are the main sod-formers of crests and ridges, while the Boutelouas characterize the higher slopes, working up to the crest and ridges. *Koeleria* seems to be more closely associated with the Boutelouas, occurring on middle slopes mainly. With these are associated three sedges and seven other grasses, which are all important as cooperating sod-formers, some of them ranking as primary species in the formation. We may mention *Carex pennsylvanica*, *C. festucacea*, and *Sporobolus brevifolius* as perhaps the more important of these. It is to be remarked that the sedges are all pre-estival, while the grasses are all estival or post-estival in their floral activity; the first facies to bloom is *Koeleria* in the estival aspect, while the Boutelouas are serotinal and the Andropogons autumnal.

Upon this facial background of grasses there progressively appear several conspicuous flowered forms of primary importance, which with numerous secondary and tertiary species serve to impart a bizarre aspect to the formation when considered as a whole and a kaleidoscopic shift with seasonal succession. In passing it is well to note that species primary in their own floral aspect may be of only secondary or tertiary importance when the formation is considered as a unit. Among these primary species we may note the ubiquitous *Antennaria campestris*; the *Spesias* and *Sisyrinchium* of middle slopes; *Amorpha canescens* upon upper slopes and ridges; *Ratibida* upon lower, and *Verbena* and *Erigeron ramosus* upon upper slopes; *Symphoricarpos* in valleys and on lowest slopes; the *Kuhnisteras* upon slopes, *K. purpurea* occupying the upper slopes, while *K. candida* extends downward upon lower slopes; *Solidago rigida* and *Helianthus scaberrimus* of great frequency and abundance; and finally *Aster sericeus* upon isolated knolls.

Among the more important of the secondary species may be mentioned *Viola pedatifida* and *Oxalis violacea* of middle and lower slopes; *Meriolix serrulata* of higher slopes; the Lithospermums of the more xerophytic portions of the formation; *Plantago Purshii* of middle slopes; *Linum rigidum* in the open association; *Potentilla Hippiana*, *Carduus undulatus*, and *Polygala alba*, which occur on middle and lower slopes; *Solidago rigidiuscula* and *S. nemoralis* upon lower and middle slopes, and *S. missouriensis* upon upper slopes mainly; and finally *Aster multiflorus* and *A. oblongifolia*.

Considering the ground association, the open association prevails over ridges and crests and extends down somewhat on slopes, passing gradually through a transitional condition into the closed association which occupies the valleys, depressions, and base of slopes, working always up or outward, displacing the open association. *Poa pratensis* establishes the most dense association, but the Boutelouas, Koeleria, and Festuca exert perhaps a more extensive influence in reducing the open association. In this connection it should be noted that the Andropogons are *par excellence* the pioneers, breaking up the xerophytic open association upon the highest and most xerophytic crests, preparing the way for the Boutelouas. It may be possible that in some cases the Andropogon bunch-grass stage was not the pioneer society, but that on account of more favorable soil moisture conditions, largely a question of drainage, the Boutelouas were the initial sod-formers. However, upon crests and ridges of excessive drainage the Andropogons have invariably preceded the Boutelouas and Koeleria. Occurring rarely in the open association is an undetermined xerophytic moss, while two species of the Basidiomycetes have been noted in the more mesophytic portions of the formation.

The enumeration of species includes 90 forms belonging to the formation proper and some 18 ruderals which work into the formation from the contiguous cultivated regions. The most abundant and prominent of the latter are *Cassia chamaecrista*, two species of Melilotus, *Hordeum jubatum* on lower slopes and moist soil; *Panicum capillare*, *Verbena bracteosa*, and *Amaranthus graecizans* of the more open associations; *Onagra biennis* of general occurrence; *Salsola* of the open association; and finally *Lepidium virginicum*, which not infrequently becomes quite abundant in the open association of

higher slopes. These ruderals are characteristically confined to marginal invasion, though they are frequently found wherever the open association makes possible their establishment. *Onagra*, however, is able to establish itself in the closed formation, as is *Potentilla monspeliensis*. *Hordeum* especially makes advance where some artificial agency has destroyed the equilibrium in rich moist stations; frequently in such cases it assumes even facial rank.

The 90 prairie elements proper have a most interesting taxonomic distribution. The composites with 29 species (32.2 per cent.) form the dominating family, comprising nearly a third of the total forms. The Gramineae number 15 species (16.6 per cent.), and though not leading in species they rank first in number of individuals. The third important family is the Leguminosae with 11 species (12.2 per cent.). Thus these three families provide 61 per cent. of the prairie elements and perhaps over 90 per cent. of the individuals. The remaining 35 species (39 per cent.) are conspicuous on account of their diverse affinities, belonging as they do to 22 different families, 14 of which have only a single representative in the formation. The families are as follows: Boraginaceae (4), Ranunculaceae (3), Cyperaceae (3), Onagraceae (3), Scrophulariaceae (2), Linaceae (2), Rosaceae (2), Oxalidaceae (2); and the following with one species each: Nyctaginaceae, Cruciferae, Umbelliferae, Iridaceae, Violaceae, Euphorbiaceae, Caprifoliaceae, Solanaceae, Labiatae, Plantaginaceae, Gentianaceae, Verbenaceae, and Polygalaceae.

The life conditions of the formation are by no means equable, and in this relation it is significant to record that only 11 per cent. of the species are annual, the majority of which produce abundant seeds and are provided with efficient means of distribution and occur mainly in the xerophytic open associations. Of the remaining 89 per cent. which are perennials, 96.2 per cent. are geophytic; *Rosa*, *Symphoricarpos*, and *Amorpha* alone are woody.

In a region characterized by strong prevailing winds it is to be noted that a high percentage of the species is wind-distributed. An analysis of this point shows that about 90 per cent. are so disseminated, some 55 per cent. showing especial facilities to this end. The great range of specific forms and their marked frequency in the formation finds an explanation in this permobility of repro-

ductive organs possessed by such a large percentage of its components.

As to pollination, 20 per cent. of the forms are wind-pollinated, while 80 per cent. have their pollen transferred by insects, the sedges and grasses comprising the former group.

Conclusions

1. The formation is a part of the Niobrara Prairie Region of CLEMENTS. In composition it is transitional. More truly a part of the prairie to the west, yet it contains several pioneer forms from the more mesophytic prairies to the south and east.

2. These two groups of elements during post-glacial migration have entered along two distinct lines of advance. The former migrated northwestward from a southwestern center of dispersal, while the latter followed a northwestern track up the Mississippi and Missouri valleys.

3. The prairie is pre-glacial in origin and is descended from the climatic prairie of Tertiary times, which arose in response to reduced precipitation caused by the upheaval of the Rocky Mountains at the close of the Cretaceous.

4. The climate is typically a prairie climate. A relatively dry resting season from October to March, in which only 16 per cent. (10.4^{cm}) of the total precipitation falls, and a moist growing season from March to September, in which 83 per cent. (49.31^{cm}) of the precipitation is distributed over sixty days, with 25 per cent. concentrated in April and May, insures a prairie formation. On the other hand, the annual low relative humidity, the dry and high winter winds accompanying high temperature, low winter rainfall, absence of a snow blanket, and the hot, dry summer of low precipitation are inimical to tree growth.

5. The absence of trees upon the prairie is primarily to be explained upon historical lines. The prairie was climatically determined and successfully and successively maintains itself against tree invasion from the edaphically determined arboreal fringes along flood plains and in ravines.

6. The northern slopes are the last to recover from winter, but are most mesophytic. It is up these slopes that the *Poa* sod and the

shrub association of *Symphoricarpus* and later *Rhus glabra* advance, preparing the way for the bur oak-slippery elm association, which likewise makes its greatest progress up these slopes from ravines and flood plains.

7. The floral activity of the formation may be approximately recorded in the following five aspects, set off by marked climatic and floral changes: prevernal, April 1 to April 25, 6 species; vernal, May 3 to May 31, 28 species; estival, June 1 to July 7, 21 species; serotinal, July 7 to August 7, 13 species; autumnal, August 7 to September 21, 22 species.

8. The prairie elements show a marked grouping into vertical layers, which correspond approximately with the floral aspects. Overtopped by the autumnal layer the sub-layers are successively those of the serotinal, estival, vernal, and prevernal.

9. There is a marked distinction in the chresard of base, slope, and crest in the prevernal, which becomes less marked in the subsequent aspects, approaching equality in the autumnal. As a result, the floral covering shows a corresponding difference upon base, slope, and crest in earlier aspects; the influence of position gradually declines, the floral covering presenting a striking similarity over the entire formation in the autumnal.